

Epiphyton or macrophyte: Which primary producer attracts the snail *Hebetancylus moricandi*?

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Abstract: Relationships between snails, epiphyton, and macrophytes are widely studied because epiphytes decrease light for macrophytes, and snails may benefit the latter when they consume epiphytes. Thus, organic compounds released by macrophytes that attract snails could be an evolutionarily advantageous mechanism. This hypothesis was tested with three species of submerged macrophytes (natives: *Egeria najas* and *Cabomba furcata*; exotic: *Hydrilla verticillata*), which were maintained in microcosms in the presence of ancyliid snails. However, the hypothesis of limpet attraction by macrophytes was rejected. Instead, epiphyton attached to *E. najas* attracted more snails than that attached to the other species. This attraction could be explained by chemical signals (organic compounds), released by certain species of algae that are detected by snails.

Key words: food web, grazers, periphyton, herbivory, chemoreception

Aquatic macrophytes are an important component of aquatic ecosystems. For example, they increase habitat complexity (Brönmark and Vermaat 1998, Thomaz *et al.* 2008) and contribute organic matter to food webs (Esteves 1998, Benedito-Cecilio *et al.* 2004, Lopes *et al.* 2007). Interactions among macrophytes, epiphyton, and invertebrates may affect the composition and distribution of epiphytic algae and invertebrate species as well as submerged macrophyte productivity and longevity (Brönmark 1985, 1989, Lodge 1986). Wetzel (2001) suggested a subtle symbiosis between these three groups and reported that herbivory is mediated by organic compounds, and that a compound that acts as an inhibitor for some snail species can stimulate others, making this type of interaction species-specific. Several authors criticized experiments using artificial macrophytes to test these interactions because unlike natural plants, artificial plants provide only substrate without chemical signals (Cattaneo and Kalff 1978, 1979, Cattaneo 1983).

The presence of these interactions has been indicated by many studies that showed that epiphyton reduced growth of macrophytes due to shading plant surfaces (Sand-Jensen 1977, Bulthuis and Woelkerling 1983, Brönmark 1985, 1989). Some freshwater invertebrate grazers, especially gastropods, are attracted by chemical signals that they detect with chemoreceptors, and food preferences between macrophytes and/or microalgae species differ among snail species. Snails also differ in assimilating different types of food (Townsend

1973, Calow and Calow 1975, Croll 1983). Many gastropods have strongly developed chemoreception and responses to signals from submerged plants. There is evidence that some species of macrophytes release compounds that attract snails, which, in turn, graze the epiphyton that colonizes the plant (Brönmark 1985, 1989). This interaction, based on chemoreception, benefits both species: the snail uses the plant as habitat for spawning, feeding, and hiding while the plant benefits from reduced competition with epiphyton. The epiphyton is also benefited, because algal removal by herbivores, a physical disturbance, promotes the regeneration of the community (Rodrigues and Bicudo 2001). Recent studies have shown that the size of plant fragments, plant age, and density of herbivores are factors that affect the submerged plant-snail interactions (Elger *et al.* 2007).

In Neotropical aquatic habitats, like the Upper Paraná River in Brazil, native snails of the family Ancyliidae are reported in association with native macrophytes, such as *Egeria najas* and *Cabomba furcata* (Thomaz *et al.* 2008). The submerged macrophyte *Hydrilla verticillata*, native from Africa and Asia, has also been recorded in habitats of the Upper Paraná River. However, specific interactions between these native snails and native and exotic plant species are unknown. In this study, we tested the hypothesis that the snail *Hebetancylus moricandi* (d'Orbigny, 1837) is attracted by particular submerged macrophytes in response to the release of chemical compounds. We expected that if this

hypothesis were true, more snails would be found in treatments with macrophytes than in epiphyton alone or in absence of macrophytes and epiphyton. The assumption behind this hypothesis is that plants and herbivores are benefited, based on previous experiments with north-temperate species (Thomas 1982, Brönmark 1985). An alternative hypothesis (also tested in our experiments) is that snails are attracted by epiphyton itself. In this case, we expected that more snails would be found in treatments with epiphyton alone than in macrophytes or in absence of macrophytes and epiphyton.

MATERIALS AND METHODS

Snails (*Hebetancylus moricandi*) and macrophytes (*Egeria najas*, *Cabomba furcata*, and *Hydrilla verticillata*) were sampled in a backwater in the Upper Paraná River floodplain, Brazil (22°45'S, 53°16'W). Invertebrates and macrophytes were collected randomly inside macrophyte stands. All sampling and experiments were completed from September to December of 2007, and each individual experiment was initiated less than three hours after sampling. Plant fragments were maintained inside transparent plastic bags at ca. 10 °C, to reduce their metabolism, until beginning the experiment.

Our experiments were based on Brönmark's (1985) work. All experiments were carried out in five "labyrinth type" acrylic aquaria measuring 30 × 15 × 15 cm. Each aquarium was created with five connected compartments (Fig. 1). Aquaria were filled with two liters of water, added from center to periphery. We then added plant fragments and algae to the compartments. Since chemicals specific to plants or algae were more concentrated in each specific compartment, we

predicted snails would choose the compartment with the preferred food.

In the first experiment, two species of submerged macrophyte were used (the native *Egeria najas* and the exotic *Hydrilla verticillata*). Three compartments were considered treatments, and the snails were introduced into the fourth, at the center of the aquarium, equidistant from the three treatments. The remaining compartment was isolated. We placed three plant fragments with epiphyton in one compartment and three without epiphyton in the other, leaving one empty compartment (control). Epiphytic material was removed from the macrophyte surface carefully with a brush and filtered water. Four snails were placed in the central compartment. The procedure was repeated nine times for each macrophyte species and each set of experiments had five aquaria, each aquarium was considered as a replicate, yielding 45 independent replicates (nine aquaria repeated five times each). The replication of each treatment was randomized in the compartments.

In a pilot experiment, we found 30 minutes to be sufficient for snail movement, and this interval was used in all experiments. Every 30 minutes, the snails' positions were recorded, plants were removed, and the water replaced. The aquaria were carefully washed with distilled water to remove attached material before every new replicate.

In a second experiment, another native submerged macrophyte (*Cabomba furcata*) was added to assess the consistency of results. The procedure described previously was repeated, but epiphyton was removed from the macrophytes and added in the compartment that had been previously isolated. At this stage, there were a total of 30 repetitions per macrophyte species. In addition to the control ("C"; compartment without material), the following treatments were: *Egeria najas* (En), *E. najas* + epiphyton (En + E), epiphyton removed from *E. najas* (E - En), *Hydrilla verticillata* (Hv), *H. verticillata* + epiphyton (Hv + E), epiphyton removed from *H. verticillata* (E - Hv), *Cabomba furcata* (Cf), *C. furcata* + epiphyton (Cf + E), and epiphyton removed from *C. furcata* (E - Cf).

The experiments were repeated a third time, but epiphyton was sampled and preserved in lugol acetic 0.5% (Rodrigues and Bicudo 2001), for further analysis of the main species of algae and their relative abundances. The organisms were counted according to Utermöhl (1958). This experiment had 15 independent replicates per macrophyte species. Two samples of epiphyton for each macrophyte species were preserved for algal identification.

The number of snails found in each compartment after 30 minutes was considered the response variable. The effects of the attraction by macrophytes and epiphyton were evaluated by analysis of variance (one-way ANOVA), considering significant values of $P < 0.05$. All assumptions were met and

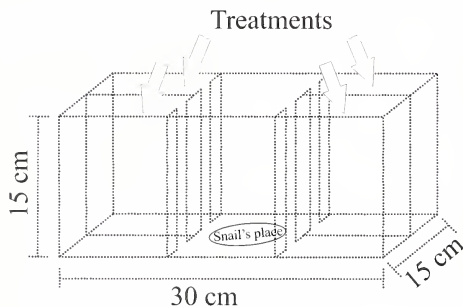


Figure 1. Aquarium used in experiments.

thus it was not necessary to transform data before statistical analysis. When differences were significant, an a posteriori Tukey test was applied.

The composition of epiphytic algae on the three macrophyte species identified in the third experiment was evaluated by a Detrended Correspondence Analysis (DCA). This analysis was applied to assess whether algae composition differed between macrophyte species.

RESULTS

In the first experiment, in which we tested the effects of *Egeria najas* on the attraction of *Hebetancylus moricandi*, the snails were more attracted by the compartment En + E (ANOVA, $F_{2,42} = 17.62$, $P < 0.001$; Fig. 2). In contrast, for the experiment with *Hydrilla verticillata*, there was no preference for any specific compartment ($F_{2,42} = 0.13$, $P = 0.87$).

The results of the second experiment showed that the treatment En + E resulted in greater colonization by snails than the treatments C and En. However, according to the Tukey test, the treatment E - En presented the highest mean snail numbers ($F_{3,26} = 12.86$, $P < 0.001$; Fig. 3). For *Hydrilla verticillata*, a slightly higher number of snails was attracted to the E - Hv compartment, but this difference was only marginally significant ($F_{3,26} = 2.89$, $P = 0.04$). In fact, these differences were not detected by Tukey tests ($P > 0.05$). In the experiment with *Cabomba furcata*, there was no significant difference between the numbers of snails attracted by each compartment ($F_{3,26} = 1.57$, $P = 0.20$) (Fig. 3). Thus, the hypothesis that the plants attract snails was rejected and the alternative hypothesis of attraction of snail by epiphyton was not rejected.

Because the second experiment showed that snails were attracted by epiphyton attached to a specific macrophyte (*Egeria najas*), we carried out a

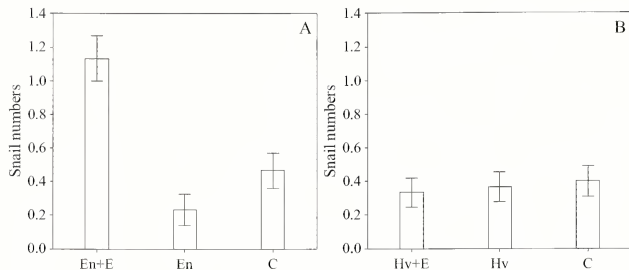


Figure 2. Mean and standard error of snail numbers attracted in the first experiment for the aquarium compartments. A, *Egeria najas*; B, *Hydrilla verticillata*. En + E, *E. najas* + epiphyton; En, *E. najas*; Hv + E, *H. verticillata* + epiphyton; Hv, *H. verticillata*; C, control compartment.

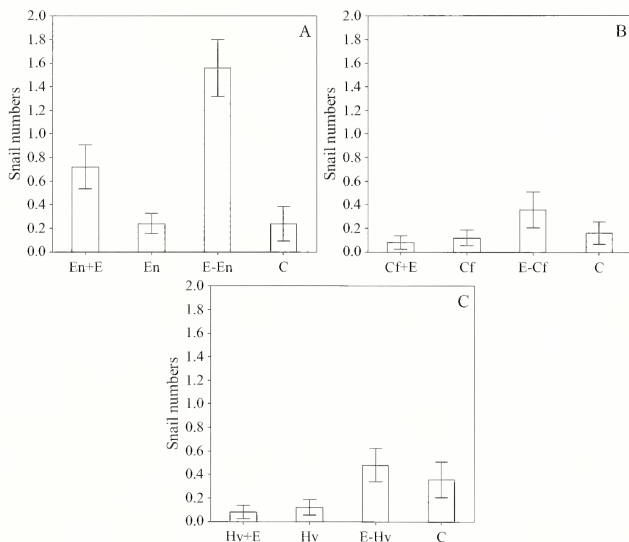


Figure 3. Mean and standard error of snail numbers attracted in the second experiment for the aquarium compartments. A, *Egeria najas*; B, *Cabomba furcata*; C, *Hydrilla verticillata*. En, *E. najas*; En + E, *E. najas* + epiphyton; E - En, epiphyton removed from *E. najas*; Hv, *H. verticillata*; Hv + E, *H. verticillata* + epiphyton; E - Hv, epiphyton removed from *H. verticillata*; Cf, *C. furcata*; Cf + E, *C. furcata* + epiphyton; E - Cf, epiphyton removed from *C. furcata*; C, control compartment.

third experiment. Similar results were obtained in this third experiment, i.e. snails were also more attracted by compartment E - En ($F_{3,11} = 6.64$, $P < 0.01$; Fig. 4). Again, for *Hydrilla verticillata* and *Cabomba furcata* there were no significant differences between treatments ($F_{3,11} = 0.79$, $P = 0.52$ and $F_{3,11} = 0.15$, $P = 0.92$, respectively) (Fig. 4).

The epiphyton from the three species of macrophytes was dominated by different species of algae (Table 1). The results of the DCA showed that the algal composition differed consistently among macrophytes (Fig. 5). In the upper right quadrant, only the algae associated with *Egeria najas* are present; in the upper left quadrant, algae associated with *Hydrilla verticillata* predominated, while in the lower quadrants algae species associated with *C. furcata* predominated. Among the main taxa associated with *E. najas* were *Cosmarium abbreviatum*, Cyanophyceae 2, and *Cymbella* sp. In contrast the epiphyton associated with *Cabomba furcata* was represented instead mainly by Chlorophyceae 3, Chlorophyceae 4, and *Cocconeis placentula*, while the algae associated with *H. verticillata* was dominated by Chlorophyceae 1, *Cocconeis pediculus*, and Cyanophyceae 3.

DISCUSSION

The hypothesis that macrophytes attract grazing snails to remove epiphyton, benefiting the plant by reducing competition for light and nutrients was rejected, and the results of three independent experiments indicated food preference by

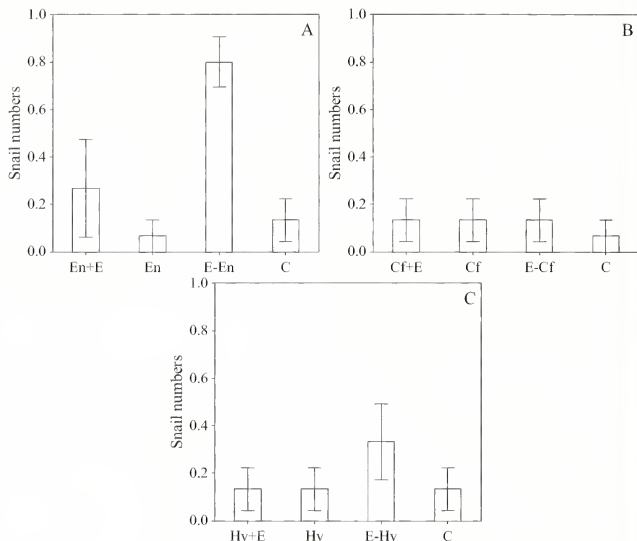


Figure 4. Mean and standard error of snail numbers attracted in the third experiment for the aquarium compartments. A, *Egeria najas*; B, *Cabomba furcata*; C, *Hydrilla verticillata*. The acronyms are given in previous figure legends.

snails for *Egeria najas* epiphyton. These results were evidenced by significant differences shown by ANOVA, revealing that a greater number of snails were attracted when epiphyton alone remained in the compartment. In addition, both the analyses of dominant groups and the DCA showed that the composition of epiphytic algae differed among the three species of macrophytes and thus, some specific group of algae attached to *E. najas* exerted more attraction (probably diatoms, which occurred in greater densities).

The importance of abundance, composition, and distribution of epiphyton for snail distribution and to the interactions between snails, epiphyton, and macrophytes in freshwater ecosystems has been shown in several papers (Lamberti and Resh 1983, Kohler 1984, McAuliffe 1984). Snails are able to select epiphyton, preferring certain algae species (Calow 1970, 1973a, 1973b, 1974). Similar results were found by Lodge (1986), who suggested significant selective herbivory by snails, since they may

Table 1. Main algal taxa encountered on macrophytes.

<i>Egeria najas</i>	<i>Cabomba furcata</i>	<i>Hydrilla verticillata</i>
Cyanophyceae 2	Chlorophyceae 3	Chlorophyceae 1
<i>Cosmarium abbreviatum</i>	Chlorophyceae 4	Cyanophyceae 3
<i>Eunotia</i> sp.2	<i>Cocconeis placentula</i>	<i>Gomphonema</i> sp.1
<i>Gomphonema gracile</i>	<i>Encyonema minutum</i>	<i>Synedra goulderi</i>
<i>Gomphonema angustum</i>	<i>Cyclotella stelligera</i>	<i>Cocconeis pediculus</i>
<i>Cymbella</i> sp.2	<i>Scenedesmus brevispida</i>	Cyanophyceae 1
<i>Cymbella</i> sp.1	<i>Gomphonema parvulum</i>	<i>Eunotia</i> sp.3
<i>Synedra</i> sp.3	<i>Synedra</i> sp.1	<i>Synedra</i> sp.2

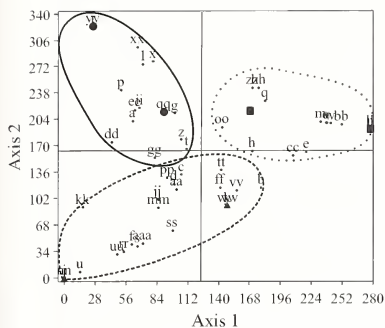


Figure 5. DCA with algal taxa and macrophyte species. a, *Achenanthidium* sp.; b, *Achenanthidium minutissimum*; c, *Aulacoseira* sp.; d, *Bulbochaete* sp.; e, *Characium* sp.; f, *Cyanophyceae* 6; g, *Chlorophyceae* 1; h, *Chlorophyceae* 2; i, *Chlorophyceae* 3; j, *Chlorophyceae* 4; k, *Cocconeis placentula*; l, *Cocconeis pediculus*; m, *Cosmarium* sp.; n, *Cosmarium abbreviatum*; o, *Chrysophyceae*; p, *Cyanophyceae* 1; q, *Cyanophyceae* 2; r, *Cyanophyceae* 3; s, *Cyanophyceae* 4; t, *Cyanophyceae* 5; u, *Cyclotella stelligera*; v, *Cymbella* sp2; w, *Cymbella* sp1; x, *Dynophyceae*; y, *Encyonema minutum*; z, *Encyonema silesianum*; aa, *Eunotia* sp1; bb, *Eunotia* sp2; cc, *Eunotia liveris*; dd, *Eunotia minor*; ee, *Eunotia* sp3; ff, *Euglenophyceae*; gg, *Fragilaria rumpens*; hh, *Gomphonema gracile*; ii, *Gomphonema* sp1; jj, *Gomphonema* sp2; kk, *Gomphonema* sp3; ll, *Gomphonema angustum*; mm, *Gomphonema* sp4; nn, *Gomphonema parvulum*; oo, *Navicula* sp.; pp, *Nitzschia* sp.; qq, *Nitzschia sigmoides*; rr, *Oedogonium* sp1; ss, *Oedogonium* sp2; tt, *Oedogonium* sp3; uu, *Scenedesmus* sp.; vv, *Scenedesmus brevispida*; ww, *Synedra* sp1; xx, *Synedra goulderi*; yy, *Synedra* sp2; zz, *Synedra* sp3; aaa, *Ulnaria ulna*; ▲, *Cabomba furcata*; ■, *Egeria najas*; ●, *Hydrilla verticillata*.

choose the local area or microhabitat where they feed. Although Lodge (1986) did not analyze epiphytic composition, he emphasized that in general diatoms were more readily consumed.

Organic compounds are released by macrophytes and algae (Gross *et al.* 1996, Mulderij *et al.* 2007, Yun *et al.* 2007), but most research has dealt with compounds that play a major role in inhibiting colonization by algae on macrophytes, or herbivory of algae by grazers. Hilt (2006) showed that native species of algae and macrophytes may have interactions related to specific compounds, and that algae can tolerate allelopathic compounds released by macrophytes. Juttner (2005) showed that some diatoms are able to reduce the activity of planktonic grazers. However, as suggested by Wetzel (2001), compounds that inhibit the activity of certain species stimulate others, and the relationship emphasized by Hilt (2006) between species of algae and macrophytes may

also occur between algae and herbivores. Thus, herbivorous species would evolve towards tolerance of the inhibitory compounds released by algae, and use them as stimuli.

Macrophytes may also determine the composition of epiphyton through release of organic compounds that inhibit certain species of algae (Brönmark and Vermaat 1998). Together with plant age and limnological features, the release of these compounds can explain why different macrophyte species are colonized by distinct epiphytic communities. The architecture and rugosity of macrophyte species are other features that also explain the dissimilarity of epiphyton found in our samples.

In the area chosen for sampling macrophytes and snails, native species of macrophytes preferentially colonized areas where light transmission is low (S. M. Thomaz, unpubl. data). At least for *Egeria najas*, the reduction of epiphyton by snails may increase light intensity over the plant surface, and facilitate the success of this species. Although this is only an inference, it has been shown that the abundance of snails can indirectly affect the pattern of macrophyte distribution, mainly in regions where the availability of light is a limiting factor (Brönmark 1989).

The composition of epiphyton attached to macrophyte species may also have been affected by their distribution in the backwater habitats. The exotic species (*Hydrilla verticillata*) is found only in the Paraná main channel, where water velocity and light transmission are higher and nutrient concentrations are lower. Native species (*Egeria najas* and *Cabomba furcata*) colonize mainly backwater habitats (Thomaz *et al.* 2009). In general, habitats with more light availability and nutrient concentrations sufficient for reproduction support elevated epiphyton growth rates (Liboriussen *et al.* 2005, Liboriussen and Jeppesen 2006).

In summary, experiments with two native species and one exotic macrophyte indicated the absence of chemoreception associated with macrophytes, and the epiphyton associated with only one species (*Egeria najas*) being responsible for the attraction of *Hebatocylus moricandi*. Based on these results, we suggest identification of organic compounds that attract snails might be searched for in the algal taxa that occurred on *E. najas* epiphyton. These results differ from those obtained in temperate ecosystems, where chemoreception seems to be associated with chemical compounds released by macrophytes (e.g., Brönmark 1985). However, further studies involving other tropical macrophyte and snail species are necessary to assess whether these results are representative for tropical aquatic communities.

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